Structural representations of fingers rely on both anatomical and spatial reference frames

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Abstract

Finger agnosia refers to a neurological condition in which patients with left posterior parietal lesions fail to identify their fingers, despite having relatively preserved abilities in sensation and skilled action. This dissociation suggests that the structural body representations (BSRs) may be distinct from sensorimotor representations. However, recent research has reported that postural changes modulate representation of hand structure, revealing dynamic interactions between structural and sensorimotor body representations. However, it is unknown how and to what extent anatomical and spatial proximity contribute to shape the hand structural representation. We investigate this question using the "*in-between*" test in which participants estimate how many unstimulated fingers are in-between two touched fingers of the left hand placed palm down. The first phalange of the participants' fingers was touched on the left or right side. Judged finger numerosity was greater when fingers were stimulated on far sides (i.e., opposite sides of the two fingers) compared to when they were stimulated on close (i.e., sides facing each other's) or mid-distance (i.e., sides facing in the same direction) sides. Therefore, fingers identification was modulated both by anatomical and spatial proximity in external space between touches. This demonstrates that BSRs rely on both anatomical and external reference frames.

Significance Statement

Traditionally body representation research focuses on dissociation between the structural body representations (BSRs) and the sensorimotor representations (e.g., body schema). Our research supports the idea of a dynamic relationship between different body representations as well as a more flexible representation of body's structure in the bodily experience, which are not fixed but varies as a function of the spatial relationships between the fingers. In the context of finger BSRs based on touch, for instance, the adoption of an anatomical reference frame is associated with neighbouring fingers, while an external reference frame with non-neighbouring fingers. Despite this reference frame bias, we show that both the anatomical and the external spatial coordinates of touch are considered when representing the fingers' structure based on touch.

Introduction

Our knowledge about the spatial relationships between body parts (e.g., limbs and fingers) is thought to be mediated by a representation known as the *body structural description*. Neuropsychological cases of *autotopagnosia*, in which patients show a specific deficit in pointing to their own or another's body parts (Semenza & Goodglass, 1985) and *finger agnosia*, a selective deficit in differentiating between one's own or another's fingers (Kinsbourne & Warrington, 1962) provide evidence for the existence of such representations. Notably, these patients often demonstrate relatively unimpaired skilled actions (Buxbaum & Coslett, 2001).

The fact that patients with autotopagnosia are impaired at identifying body parts, despite unaltered sensation and skilled action has traditionally been interpreted as evidence that structural body representations (BSRs) are mediated by mechanisms different from sensorimotor representations, such as the body schema (Anema et al., 2008; de Vignemont, 2010; Longo, Azañón, & Haggard, 2010; Schwoebel & Coslett, 2005; Tamè, Azañón, & Longo, 2019). This is intuitive, since body posture changes constantly but the structural configuration of the body remains stable. Recent evidence from our laboratory has shown that BSRs are not as fixed as previously believed, but are modulated by the relative positions of body parts - i.e., fingers (Tamè, Dransfield, Quettier, & Longo, 2017), suggesting that "on-line" and "off-line" representations of the body are not completely distinct, but may dynamical interact.

A classic measure of finger agnosia is the so called '*in-between*' test (IBT) in which participants judge the number of unstimulated fingers in-between two simultaneously touched fingers (Kinsbourne & Warrington, 1962). We recently used this task to show that the judged number of fingers in-between is generally underestimated, though increases when the fingers are splayed compared to when they are pressed together (Tamè, Dransfield, et al.,

2017). This demonstrates that BSRs are influenced by finger posture, or the physical distance between fingers in external space, or possibly both. This highlights the importance of understanding how body representations dynamically interact, in addition to how they differ.

Behavioural and neurophysiological studies have identified various reference frames used for tactile localisation, e.g., relative to the head (Ho & Spence, 2007; Pritchett, Carnevale, & Harris, 2012), trunk (Heed, Backhaus, Röder, & Badde, 2016), gaze (Harrar & Harris, 2009; Medina, Tamè, & Longo, 2018) or specific body part (Benedetti, 1988) as well as musculo-skeletal factors (Sadibolova, Tamè, & Longo, 2018), depending on task demands (Harrar & Harris, 2009; Pritchett & Harris, 2011; Tamè, Wühle, Petri, Pavani, & Braun, 2017; Yamamoto & Kitazawa, 2001). Touch is originally encoded in anatomical (skin) coordinates but then rapidly and automatically recoded into external coordinates (*spatial remapping*) (Azañón, Longo, Soto-Faraco, & Haggard, 2010; Azañón & Soto-Faraco, 2008) and according to some recent findings, both anatomical and the external coordinates are available in parallel (Badde & Heed, 2016; Tamè, Wühle, et al., 2017). This suggests a flexible use of reference frames, which vary as a function of the real-time physical distances of the body in space. Moreover, previous studies suggest that the location of the hands – but not the fingers – is recoded into an external spatial reference frame, and that differentiation between fingers may rely more on anatomical coordinates (Benedetti, 1985; Haggard, Kitadono, Press, & Taylor-Clarke, 2006). By contrast, another study found that finger location is coded in external coordinates both with respect to the hand and as an individual body part (Riemer, Trojan, Kleinböhl, & Hölzl, 2010). Therefore, it remains unclear how the fingers' locations relative to each other are represented and identified.

Here we explored the nature of BSRs and the spatial reference frames used for finger structural representation using an adapted version of the in-between test in which we

stimulated the sides of fingers (Figure 1A). Participants' task was to judge how many unstimulated fingers were touched in-between the two touched fingers. We will estimate their judgments as distance in finger space, that could be zero, one, two or three. This allowed us to dissociate the distance between stimuli in anatomical space (i.e., how many fingers are between the two stimuli) and external space (i.e., how many cm are between the two stimuli). If BSRs primarily rely on anatomical coordinates, we should observe the same pattern of results (e.g., underestimation of the number of fingers in-between) across all fingers regardless of the side of the fingers stimulated – i.e., left or right. By contrast, if BSRs rely also on external spatial coordinates, stimuli presented on close sides of two fingers should produce smaller estimates than those presented on far sides, even when the actual number of fingers in between remains constant.

Method

Participants. Thirty people (20 females; aged 18 to 46, M±SD = 29.8 ± 9.1) participated. Participants reported normal touch and normal or corrected to normal vision. All were right-handed, as assessed by the Edinburgh Inventory (Oldfield, 1971; M = 90, range 47 – 100). The study was approved by the local ethics committee. A power analysis showed that our study is appropriately powered to identify a comparable effect of stimulus location (see supplementary material).

Apparatus and stimuli. Tactile stimuli were delivered for **5** ms on the non-thumb fingers of the left hand using eight solenoid tappers (rounded tip, 9 mm diameter, 0.2-mm skin contact; M&E Solve, UK) driven by a 9 V square wave (Figure 1A). A sheet of black cardboard prevented vision of the hand and a white marker served as a fixation point (~ 1cm^2)

to control for head (cf. Ho & Spence, 2007) and gaze (cf. Medina, Tamè, & Longo, 2018) positions. Fingers were positioned at 1.**5** cm distance between each other.

Procedure. Procedures were similar to our previous study (Tamè, Dransfield, et al., 2017). A detailed description of procedures is in supplementary material. On each trial a pair of tactile stimuli was presented simultaneously. Between trials there was a variable inter-stimulus interval, ranging from 1200 to 2200 ms, after participant's response. By delivering pairs of tactile stimuli, in different trials we had two possible fingers sides stimulated divided in three main categories: 1) close (Figure 1A green dots); 2) at mid-distance (Figure 1A white dots); 3) far (Figure 1A red dots). Moreover, a single finger could be stimulated on its two sides, note that this possibility is not depicted in Figure 1A and data will be analysed separately as it was not critical for the main purpose of our study. Finally, as mentioned above the distance in finger space could be zero, one, two or three. The participant's task was to estimate how many unstimulated fingers there were in-between the two touched fingers, responding as quickly and accurately as possible. Reponses were given verbally and no feedback was provided. When the same finger was stimulated, they were instructed to respond "*same*". If no response was made after 3000 ms, a new trial started.

Data analysis. Responses were coded and averaged as DISTANCE IN FINGER SPACE (i.e., Zero, One, Two, Three) and the FINGER SIDE stimulated (Close, Mid-distance, Far). The average response numerosity and reaction times (RT) were entered in two separate two-way analyses of variance (ANOVAs) with FINGER SIDE (Close, Mid-distance, Far) and DISTANCE IN FINGER SPACE (One, Two, Three) as within-participant factors. To determine the contribution of both anatomical reference frames and spatial distance, we performed a multiple regression analysis including number of fingers in-between and the physical distance (in cm) between the fingers as separate predictors (for a complete description of the multiple regression

analysis and of how we estimated the average width of the fingers and distance between the fingers in external space see Supplementary Material). Note that the level "*Zero*" was not included in the analyses (see Supplementary Material) due to the experimental design and purpose of the study. The raw data are publicly available at https://osf.io/k6q5h.

Results

There was a significant interaction between the factors DISTANCE IN FINGER SPACE and FINGER SIDE, $F(2.39, 69.20) = 7.02$, $p < 0.001$, MSE= 0.035, $\eta_p^2 = 0.20$. As Figure 1B illustrates, participants generally underestimated the number of unstimulated fingers. Despite overall underestimation, this interaction shows the presence of the same qualitative pattern for each number of fingers in-between in which when the far finger sides were stimulated numerosity judgments were higher (M ± SE= 1.95 ± 0.04) compared to when close (M ± SE= 1.57 ± 0.06, $t(29) = 8.55$, $p < 0.001$, $d_z = 1.56$) and mid-distance finger sides (M ± SE= 1.75 ± 0.05, $t(29) = 7.20$, $p < 0.001$, $d_z = 1.31$) were stimulated. The difference between trials involving close and mid-distance finger sides was also significant, $t(29) = -6.69$, $p < 0.001$, $d_z = 1.22$). The interaction shows that these effects decrease with the number of fingers in between. Our participants' judgements closely corresponded to the actual changes in the spatial distance between stimuli, when there were one or two fingers in-between. This suggests that BSRs in such a context, rely also on external spatial coordinates.

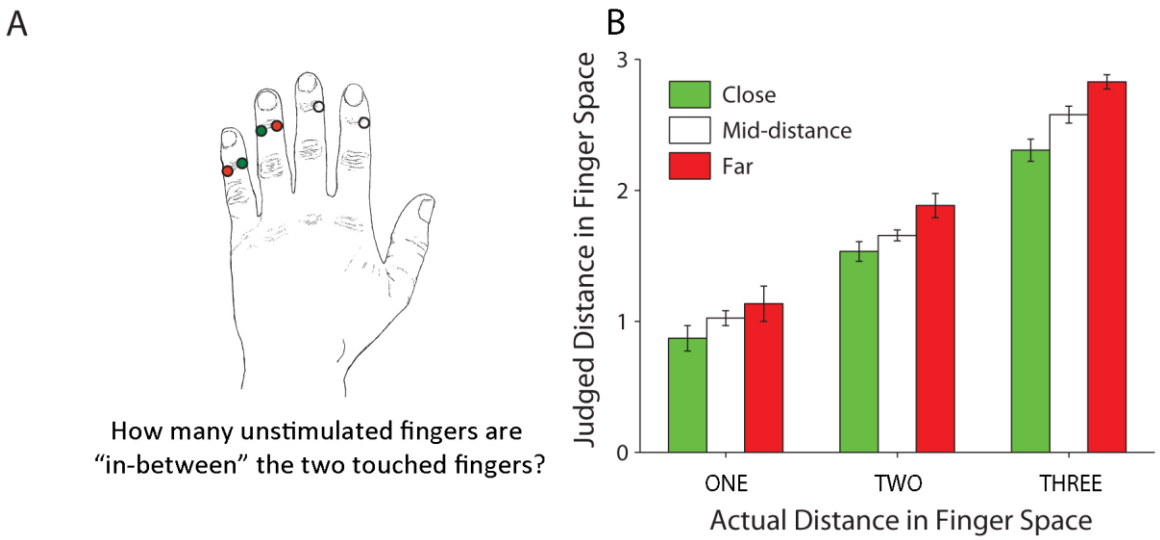

Figure 1. The "in-between" task (A) for the conditions in which close finger sides were stimulated (green circles), mid-distance finger sides (white circles) and far finger sides (red circles) were stimulated. (B) Judged finger numerosity for the different distance in finger space as a function of fingers' side. Error bars indicate 95% within participants Confidence Intervals (95%CI) (Loftus & Masson, 1994).

Moreover, as expected there were significant main effects of DISTANCE IN FINGER SPACE, $F(1.25, 36.27) = 383.55$, $p < 0.001$, MSE= 0.230, $\eta_p^2 = 0.93$, and FINGER SIDE, $F(1.34, 38.73) = 62.43$, $p < 0.001$, MSE= 0.077, $\eta_p^2 = 0.68$, which were, however, subsidiary to the higher order interaction described above (see Supplementary Material for detailed description of the main effects, the same analyses performed on RTs as well as a series of one-sample t-tests of the judged numerosity against "0" to further explore the different pattern of results when there were no fingers in-between).

Moreover, using a least-square multiple regression analysis to model the contributions of distance in anatomical space and in external space (see Supplementary Material), we found that both the anatomical and the external spatial coordinates of touch are used for finger differentiation based on touch.

Discussion

We used the in-between test to examine the reference frames used by structural body representations when coding touch on the fingers. To this aim, we stimulated different sides of the fingers, allowing us to dissociate distance in finger space versus distance in external space. Judgements were higher when the far sides were stimulated compared to when mid-distance or close sides were stimulated. This shows that judgments are affected not only by distances in "offline" anatomical space (i.e., by how many fingers are actually between the stimulated fingers), but also by distance in "online" representations of the body's location in external space.

We observed a somewhat different pattern of performance when neighbouring fingers were stimulated. Indeed, participants occasionally judged stimuli on adjacent sides of neighbouring fingers as belonging to the same finger. Moreover, unlike in any other condition tested, participants overestimated finger space when far finger sides of neighbouring fingers were stimulated. Although, touch is localised using anatomical coordinates as shown by the progressive increment in the judgments of finger space, external coordinates appear also to influence the tactile location on the fingers. These results corroborate the notion that both the anatomical and the external spatial coordinates significantly contribute to finger representation.

Overall, these results demonstrate that both anatomical and external spatial coordinates are used when representing the relative spatial location of fingers through touch. This provides further evidence that BSRs are not static and that the skin proximity between the stimulated fingers affects the way in which the fingers are represented. Specifically, the relative position of fingers and stimulus location are clearly considered when non-neighbouring fingers are touched. We observed a monotonic increase between judged

number in finger space and the relative distance between touches on the fingers in the external space.

Tactile identification of neighbouring fingers

The pattern of responses when finger space distance was one suggests poor differentiation between neighbouring fingers. Indeed, when close finger sides were stimulated participants tended to perceive the touches on the same finger. This is consistent with the topography of SI where neighbouring fingers have more highly overlapping receptive fields (e.g., Iwamura, Tanaka, Sakamoto, & Hikosaka, 1983), patterns of representational similarity in sensorimotor cortex (Ejaz, Hamada, & Diedrichsen, 2015), and tactile mislocalisation between fingers (Manser-Smith, Tamè, & Longo, 2018; Schweizer, Maier, Braun, 2000; Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001) as well as previous findings using the "in-between" task (Rusconi, Gonzaga, Adriani, Braun, & Haggard, 2009; Tamè, Dransfield, et al., 2017).

Neighbouring finger stimulation resulted in overestimation of finger numerosity, but only when far finger sides were stimulated. Consistent with previous research on tactile mislocalisation (e.g., Schweizer et al., 2001), participants most likely attributed the far, presumably functionally unrelated, finger sides to the closest neighbouring finger. Similarly, when directly close finger sides were stimulated with one fingers space, participants underestimated finger numerosity. This pattern suggests that they misattributed touch delivered to directly close finger sides as occurring on the same finger.

By contrast, when mid-distance finger sides were stimulated, neither under- nor over-estimation was present. In this condition, the distance on the skin is the same as when fingers are touched on the centre rather than on the sides (e.g., see our previous study Tamè,

Dransfield, et al., 2017). This indicates that the distance between touches on the fingers is perceived in the same way regardless of the side of finger stimulated for neighbouring fingers. This however does not fully explain the variable performance observed with the different fingers' parts (i.e., close, mid and far sides) stimulated on neighbouring fingers and points to complex spatial relations in body part differentiation. Neighbouring fingers could potentially be considered as a special case in finger representations where relation to other fingers is not necessary for solving the task, so no re-mapping into external coordinates occurs.

Tactile identification of non-neighbouring fingers

Stimulation of non-neighbouring fingers produced overall underestimation of the finger space and was modulated by the finger side. Note that for the three fingers space condition this can be over weighted given that there could be no more than three spaces. Critically, finger space judgments were higher when far finger sides were stimulated compared to when the fingers were stimulated on mid-distance or close finger sides. Therefore, judgments corresponded to the physical distance between stimuli in external space. This suggests dominance of the external spatial reference frame when touches occur on non-neighbouring fingers, though, the anatomical reference frame also had a significant influence on the distance judgments. The important role played by external spatial coordinates in the perceived position of body parts relative to each other through touch is supported by the presence of several potential sources of top-down and bottom-up information (Palermo, Di Vita, Piccardi, Traballesi, & Guariglia, 2014; Tessari, Ottoboni, Baroni, Symes, & Nicoletti, 2012) that interact and jointly contribute to structural body representations. A recent fMRI meta-analysis by Di Vita and colleagues (Di Vita, Boccia, Palermo, & Guariglia, 2016) showed that primary somatosensory cortex and the

supramarginal gyrus are selectively active in the presence of non-action-oriented body representations, whereas the primary motor cortex and the extrastriate body area are selectively active for action-oriented body representations.

Interplay of reference frames

Our findings suggest that anatomical and external spatial reference frames are integrated and used to locate touch on the fingers and that these coordinates are used in finger structural representation based on touch. Evidence discussed earlier supports this idea by demonstrating that we can employ multiple reference frames to represent touch on the body or body parts in space (e.g., Badde & Heed, 2016; Haggard et al., 2006; Tamè, Farnè, & Pavani, 2011b). It has been proposed that spatial touch perception is achieved through the integration of multiple location codes that are weighted on the basis of the availability and reliability of all the spatial information (Badde & Heed, 2016). Recently, Badde and colleagues (Badde, Röder, & Heed, 2019) have shown systematic patterns of confusions between touches on different limbs, based on homology (e.g., confusions between hand and foot), laterality (e.g., confusions between the right and left feet), and one limbs' canonical location in space. Such errors suggest that touch may be coded in terms of a set of abstract features, rather than (or in addition to) a continuous somatotopic map (Azañón & Longo, 2019).

In conclusion, our findings clearly demonstrate that a combination of the anatomical and the external spatial coordinates of touch are used in finger structural representation based on touch on the fingers of the same hand. The present study supports the view that body structural representations are more flexible rather than fixed as previously thought.

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